

## Research Paper

# The giant emucaridid *Tafilocaris ordovicica* gen. et sp. nov. (Euarthropoda, Nektaspida), a peri-Gondwanan ‘Cambrian’ survivor in the Upper Ordovician Tafilalt Biota of Morocco

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## ABSTRACT

Emucaridids are small, non-biomineralised, nektaspid trilobitomorph arthropods so far only known for the Cambrian. Their bodies are made up of a cephalic shield, a small number of thoracic segments and an elongate pygidium, larger than the cephalon. Here we describe a new emucaridid, *Tafilocaris ordovicica* gen. et sp. nov. from the early Late Ordovician (Sandbian 1), Bou Nemrou locality (Jbel Tijarfaïouine) of the Tafilalt Lagerstätte of Morocco. The two specimens of this new fossil arthropod are preserved in medium-grained sandstones and are about 150 mm long and 100 mm wide, making it almost twice the size of the largest nektaspid known to date, *Naraoia magna* from the Burgess Shale (British Columbia), and 5–25 times larger than other species in the Family Emucarididae. This concurs with observations made in other high palaeolatitude Ordovician taxa, where polar gigantism has been described in some radiodonts, trilobites and palaescolecid worms from different Ordovician biotas of Morocco and Portugal. The stratigraphical range of the new taxon is also compared with other Nektaspida of Cambrian and Ordovician age and reveals the survival of the Family Emucarididae beyond the Cambrian, and its expansion from Eastern Gondwanan and South China tropical waters to Southwestern Gondwanan polar environments.

## 1. Introduction

Ordovician Konservat-Lagerstätten of Morocco include two renowned biotas of high international interest (Van Roy, 2006a, 2011). The older one is the Fezouata Biota of Early Ordovician (late Tremadocian to late Floian) age, which is preserved in shale and includes sponges, priapulids (Martin et al., 2016a) and abundant non-trilobite arthropods, such as large radiodonts, marrellomorphs (Laibl et al., 2023), nektaspids and aglaspids (Ortega-Hernández et al., 2016), reminiscent of those of the Cambrian Burgess Shale and Chengjiang biotas (Botting, 2007; Van Roy et al. 2010, Van Roy et al., 2015b; Martin et al., 2016b; Lefebvre et al., 2016, 2020; El Hariri et al., 2022; Saleh et al., 2022; Potin et al., 2023). The younger one is the Tafilalt Biota, of Late Ordovician (early Sandbian to mid Katian age), where a diverse echinoderm and trilobite fauna occur associated with several weakly or non-biomineralised metazoans preserved in medium- to coarse-grained

sandstones, in a style more similar to the Ediacaran fossils of the Flinders Ranges in Australia (Van Roy, 2006a, 2011; Samuelsson et al., 2001). The shelly fauna, recently described or re-examined by several authors (Hunter et al., 2022), occurs together with relatively abundant articulated scleritomes of machaeridian annelids (Vinther et al., 2008, Parry et al., 2023). The non-biomineralised or weakly biomineralised fossils occurring in the Tafilalt Biota include paropsonemid eldonioids (MacGabhann et al., 2019), palaescolecid worms (Gutiérrez-Marco & García-Bellido, 2015; García-Bellido & Gutiérrez-Marco, 2023) and several non-trilobite arthropods such as cheloniellid arthropods, plus very rare aglaspids, eurypterids and a possible nektaspid (Van Roy, 2006a, b; Van Roy in Lefebvre et al., 2022a).

The new taxon described here is represented by two complete specimens, which, not only increases the generic diversity of emucaridid nektaspids, but also extends their stratigraphic range by almost 60 Ma, from Cambrian Series 2 to the Late Ordovician, while expanding their

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biogeographic occurrence from the low-latitude realm of Northern Gondwana and South China to the polar environments of Southern Gondwana.

The giant size reached by this new arthropod, at least five times larger than other emucaridids, is also noteworthy and may be related to palaeogeography. The south Gondwanan placement of Morocco and the Iberian Peninsula, reconstructed at a high palaeolatitude of c. 80° S during the Ordovician (Torsvik & Cocks, 2017, figs 6.2 and 6.9), has been argued as an explanation for the cases of cold-water gigantism described in several invertebrate groups of this area (Saleh et al., 2021), including trilobites (Gutiérrez-Marco et al., 2009), radiodonts (Van Roy et al., 2015a), bryozoans (Jiménez-Sánchez et al., 2015), conulariids (Van Iten et al., 2022), and palaeoscolecid (García-Bellido & Gutiérrez-Marco, 2023).

## 2. Materials and methods

The studied material consists of two complete, fully articulated specimens of a giant, weakly-biomineralised arthropod preserved as part and counterpart in medium- to coarse-grained sandstone. They occurred parallel to bedding plane at the bottom of a temporal deep trench which in 2017 lied in the northern extension of the main sandstone quarry made for commercial exploitation of fossils at the site of Bou Nemrou (31° 19' 37.4" N, 04° 31' 35" W). This is a well-known palaeontological site, located northeast of the Ksar (village) Tamarna and about 10 km to the north of the Alnif-Rissani road (Fig. 1). The site has been labelled KR-1, CRF-4 or ECR-F4 in several papers, most of them devoted to the echinoderm assemblage (Regnault, 2007; Hunter et al., 2010; Lefebvre et al., 2010, 2011, 2022b; Sumrall & Zamora, 2011). The studied material was apparently discovered towards the end of 2017 by a digging team led by Mr. Lahsa Ouzmou (Ksar Tamarna) and purchased in February 2018 from a private seller who offered Bou Nemrou fossils in Erfoud. This material is now deposited at the Museo Geominero (IGME-CSIC) in Madrid and catalogued with the prefix MGM, plus the X suffix as part of the non-Spanish fossil subcollection.

The Bou Nemrou locality is stratigraphically placed at the top of the First Bani Group, in beds equivalent to the Izzeguiene Formation (Destombes et al., 1985), having been dated as early Sandbian (basal Late Ordovician) by means of chitinozoans and shelly fossils (Gutiérrez-Marco et al., 2003). More detailed geological information on the

stratigraphy, age, sedimentary environment and taphonomy of the fossil locality has been presented in previous works (Gutiérrez-Marco & García-Bellido, 2015; MacGabhann et al., 2019; Gutiérrez-Marco et al., 2022a,b).

Specimens are preserved as internal, external or composite moulds in medium- to coarse-grained sandstones, usually contrasting in yellow to brownish colours from the matrix. This can suggest some degree of pyritization of arthropod cuticles and subsequent weathering to iron oxides. The non-exposed parts of specimens were mechanically prepared with a Paleotools Micro-Jack 6 compressed-air vibration tool equipped with a fine stylus. Study of surface characters was made through latex casts taken from external and internal moulds.

Most of the illustrated specimens were whitened with magnesium oxide and photographed using a Canon EOS 7D digital camera with Canon Macro EF5 60 mm lens, both dry with low angle incident NW lighting and also immersed in water, to increase the contrast of the preserved features. Camera lucida drawing was made with an Olympus SZX10 binocular microscope. Figures were designed with Adobe Illustrator 24.6 and assembled with Adobe Photoshop 24.6.

## 3. Fossil arthropods from the Bou Nemrou assemblage

The more common arthropods of the Tafilalt Biota recorded at the 'Bou Nemrou' assemblage are trilobites (Gutiérrez-Marco et al., 2022a). This group comprises eleven species at the locality, belonging to ten genera, some of them showing interesting cases of exceptional preservation of digestive structures and possible muscle scars (Fatka et al., 2013; Gutiérrez-Marco & García-Bellido, 2015; Budil & Fatka, 2022; Gutiérrez-Marco et al., 2022a). The trilobites from Bou Nemrou show strong relationships with trilobite assemblages from the Dobrotivian and lower Berounian sandstone facies of Bohemia, also suggested by the common record of the Dobrotivian palaeoscolecid genus *Gamascolex* (Kraft & Mergl, 1989; Gutiérrez-Marco & García-Bellido, 2015), as well as by the lower Berounian cheloniellid genera *Duslia* and *Triopus* (Van Roy, 2006a; Gutiérrez-Marco et al., 2020; Lefebvre et al., 2022a).

In contrast with the trilobite assemblage from Bou Nemrou, the non-trilobite arthropod fauna has never been properly described (Alessandrello & Bracchi, 2006), despite the weakly sclerotised cheloniellid genus *Duslia* (Fig. 2) occurring in very high numbers in the sandstone beds and showing clear resemblances with the Czech species

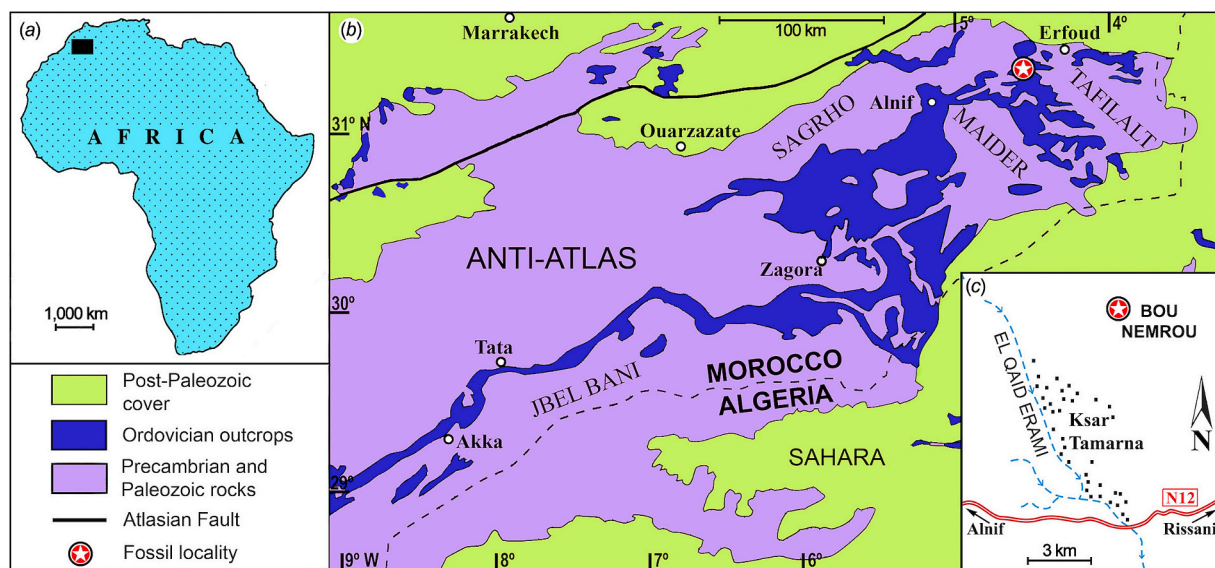
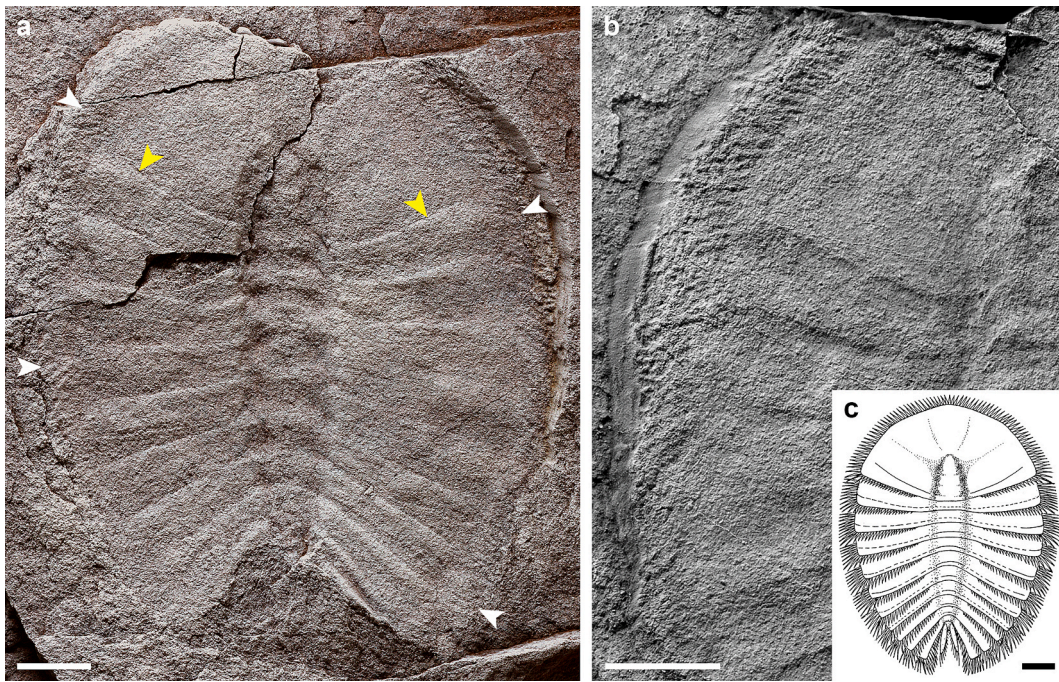


Fig. 1. General, regional and local maps for fossil locality. a. Map indicating the position of the studied region in Africa. b. Geological sketch map of the central and eastern Anti-Atlas of Morocco, showing the position (star) of the Jbel Tijarfaiouine area. c. Sketch map of the area around the 'Bou Nemrou' site (star). All from Gutiérrez-Marco & García-Bellido, 2015.



**Fig. 2.** *Dustedia insignis* Jahn, 1893 from the ‘Bou Nemrou’ site (top of the First Bani Group), early Sandbian, Tafilalt Biota. a–b. Specimen MGM-7908X. a, concave, external mould. b, latex cast. Whitened with magnesium oxide; white arrowheads point to densely spinose cephalic shield and tergite fringes, yellow arrowheads point to procurved posterior cephalic margin. c, *Dustedia insignis* reconstruction from Chlupáč (1988). Scale bars 10 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*D. insignis* Jahn, 1893, from the Letná Formation of Bohemia (Chlupáč, 1988, 1999; Rak, 2009). Previously, Lefebvre et al. (2022a, p. 16) had indicated that the Moroccan record possibly belongs to a different species, although its quality of preservation is generally not as good as that of the Czech material; however, new specimens from Bou Nemrou (Fig. 2) display sufficient characters to suggest that both forms could be conspecific (L. Laibl., written comm., 3 April 2025).

There are other rare non-trilobite arthropods found in the Bou Nemrou assemblage, such as the poorly known cheloniellid *Triopus* sp. (Van Roy, 2006b; Lefebvre et al., 2022a). This genus was previously represented by a single incomplete specimen from Bohemia (Chlupáč, 1988; Van Roy et al., 2022). Additional rare finds from Bou Nemrou (Lefebvre et al., 2022a) report a single aglaspidid specimen showing some similarity to the Cambro-Ordovician genus *Tremaglaspidis*, plus a nektaspid (studied here), and some fragmentary material possibly belonging to chelicerate arthropods including a possible carcinosomatid eurypterid and an undetermined xiphosurid.

## 4. Results

### 4.1. Systematic Palaeontology

Phylum EUARTHROPODA Lankester, 1904.

Subphylum ARTIOPODA Hou & Bergström, 1997.

Superclass TRILOBITOMORPHA Störmer, 1944.

Order NEKTASPIDA Raymond, 1920.

Family EMUCARIDIDAE Paterson, Edgecombe, García-Bellido, Jago & Gehling, 2010.

*Included taxa:* *Emucaris fava* Paterson, Edgecombe, García-Bellido, Jago & Gehling, 2010 (type genus), *Kangacaris zhangii* Paterson, Edgecombe, García-Bellido, Jago & Gehling, 2010, both from the Cambrian Series 2, Stage 4 Emu Bay Shale Lagerstätte of Kangaroo Island (Australia), and *Kangacaris shui* Zhang, Fu & Dai, 2012 from the Series 2, Stage 3 Chengjiang Lagerstätte (Helinpu Formation) of Yunnan (China).

*Tafilocaris* gen. nov.

*Etymology:* Tafilo, after the Tafilalt Biota, and –caris, shrimp (f.

Latin), a common suffix for Palaeozoic arthropods.

*Type species:* *Tafilocaris ordovicica* gen. et sp. nov.

*Diagnosis:* Very large emucaridid with semielliptical cephalic shield, three thoracic segments, and acuminate pygidium about ten percent longer than the length of cephalic shield. Body domed in lateral profile, lacking raised axis. Thoracic tergites with posterolaterally deflected pleural region and faintly acute posterior corners.

*Tafilocaris ordovicica* gen. et sp. nov.

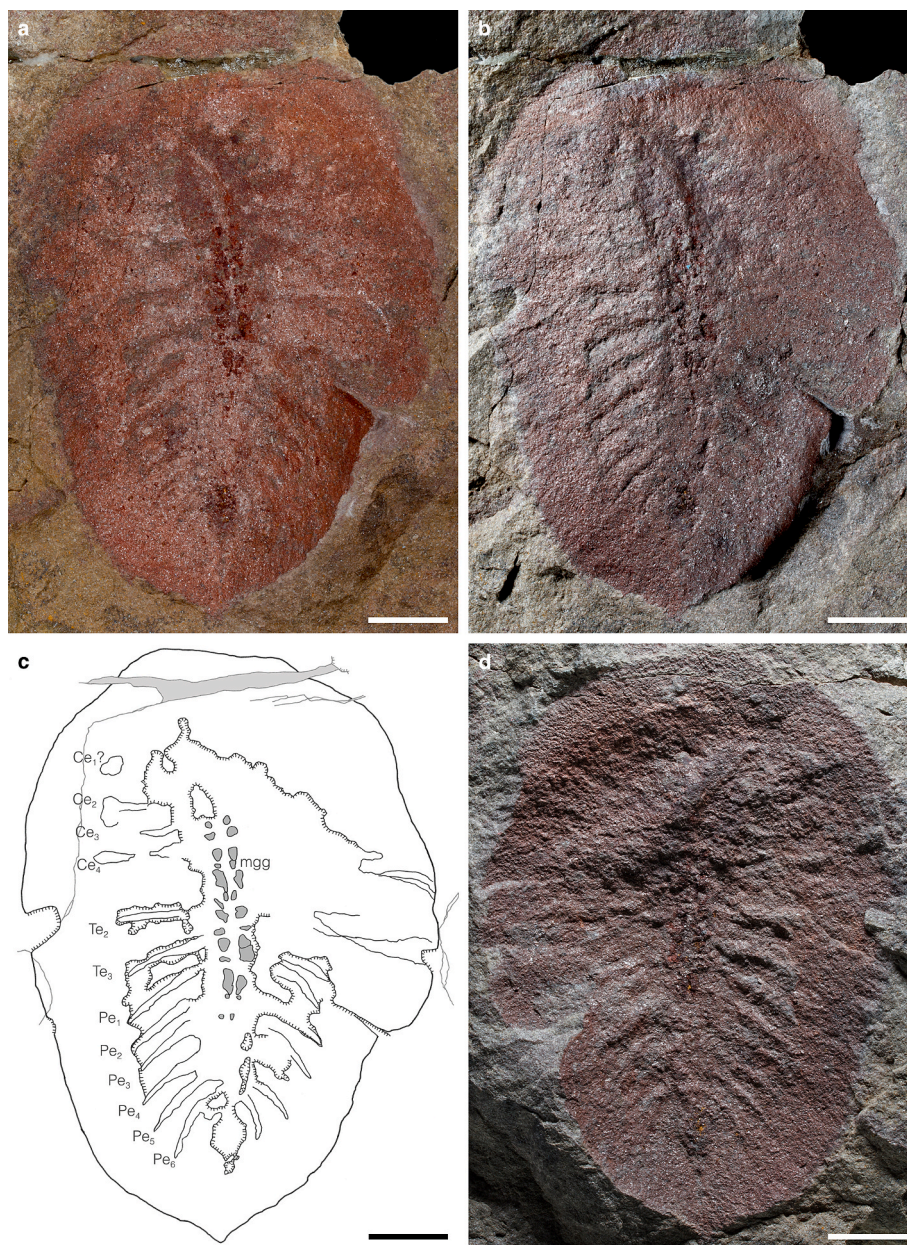
Figs. 3–6, Table 1

*Etymology:* After the Ordovician geological period in which it lived, to emphasise the longevity of the family, so far only known from the Cambrian.

*Diagnosis:* As for genus.

*Material and locality:* Holotype (Fig. 3), MGM-7201Xa (convex part, Figs. 3a, b) and MGM-7201Xb (concave counterpart, Fig. 3c) and paratype (Fig. 4), MGM-7755Xa (convex part, Fig. 4d) and MGM-7755Xb (concave counterpart, Figs. 4a, b) were collected from ‘Bou Nemrou’ locality of the Tafilalt Lagerstätte, early Sandbian, Morocco.

*Description:* The length (sag.) of the holotype is 151 mm (Fig. 3), while the paratype is 157.5 mm long (Fig. 4 and Table 1). The maximum exoskeletal width (tr.) is 103 mm in the holotype and 106 mm in the paratype (across  $T_{S2}$ ), thus 68 and 67% of the sagittal length respectively. The specimens are convex in lateral view, with a maximum height of 19.30 mm in the holotype and 10 mm in the paratype. The paratype is the only specimen in which the cephalic, thoracic and pygidial lengths can be determined (Fig. 4), with 68, 15.5 and 74 mm respectively (Table 1). In this specimen, the cephalic shield is 43% the length of complete exoskeleton; the length of cephalic shield is around 66% of its width. When overlaying the outlines of holotype and paratype (Figs. 3c and 4c, respectively), proportions in both are very similar. The anterior margin of the cephalic shield is evenly rounded and shows no evidence of a doubleure. Using as reference the size of second and third thoracic tergites, the cephalic shield would medially overlap half to two thirds of the first thoracic tergite (dotted line in Fig. 5). The pleural region of the thoracic tergites is posterolaterally deflected and widening distally, where length (sag.) reaches 8–9 mm. The pygidial length in the paratype

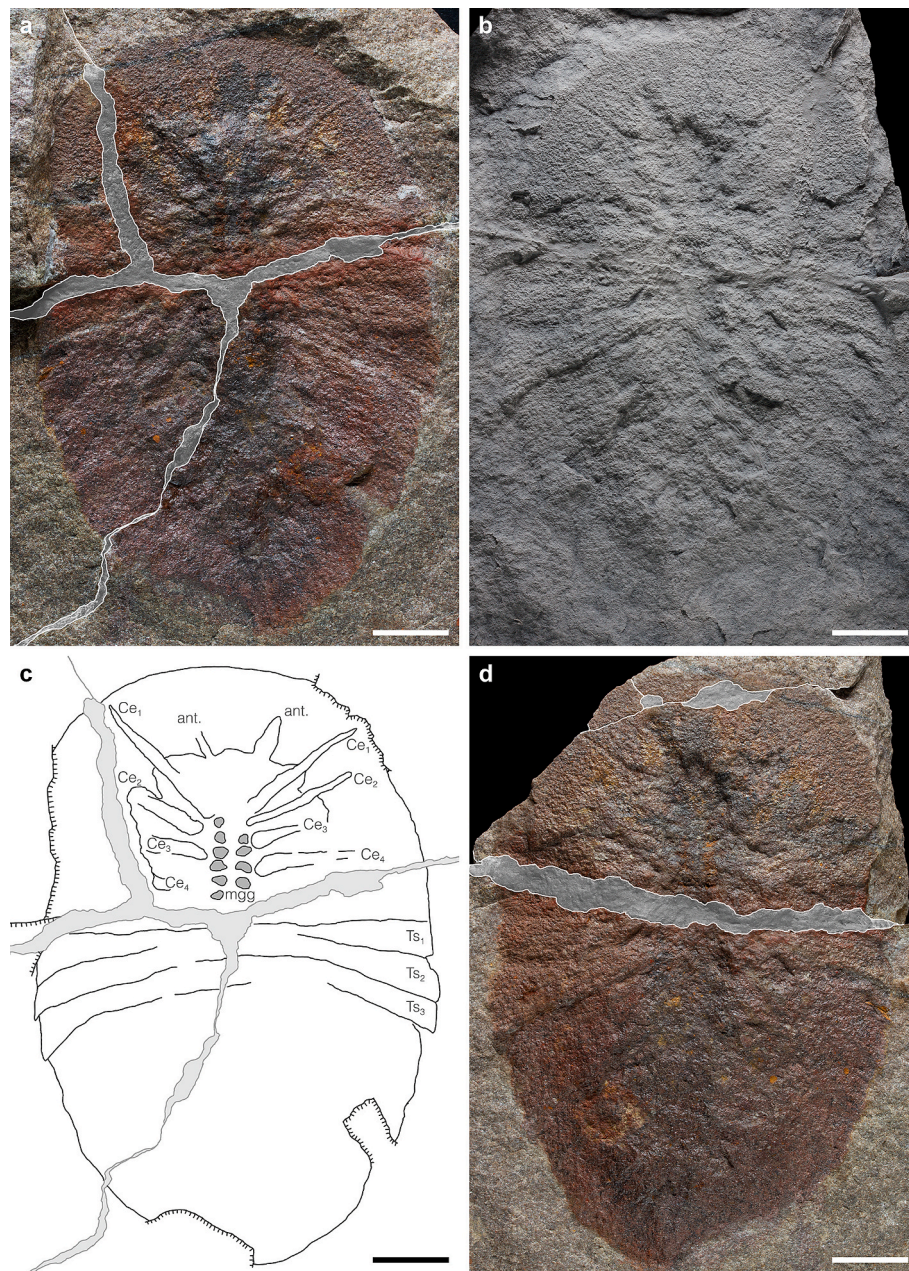


**Fig. 3.** Holotype of *Tafilocaris ordovicica* gen. et sp. nov. (MGM-7201Xa + b), from the ‘Bou Nemrou’ site (top of the First Bani Group), early Sandbian, Tafilalt Biota. a. Convex part MGM-7201Xa, under water, enhancing colour contrast between specimen and matrix. b. Convex part, MGM-7201Xa, low-angle lighting from NW. c. Composite *camera lucida* drawing of part and counterpart, minor reconstruction of the part indicated in light grey. d. Concave counterpart, MGM-7201Xb, low-angle lighting from NW. Abbreviations: Ce<sub>n</sub>: Cephalic endopods; mgg: midgut glands; Pe<sub>n</sub>: Pygidial endopods; Te<sub>n</sub>: Thoracic endopods. Scale bars 20 mm.

is 1.31 times longer than wide, 47% length of complete exoskeleton; it is obdeltoid in outline, has gently convex margins and a rounded acuminate posterior end. Appendages present mostly as breakages through the dorsal carapace. Not all the cephalic appendages can be unequivocally recognised due to faint preservation in the holotype (Figs. 3a, c) or rock breakage in the paratype (Figs. 4a, c). However, upon combining the evidence from both specimens, the continuous presence of paired midgut glands (see below) and the expected equidistance distance between body appendages (Table 1), we argue that the species had five pairs of biramous cephalic appendages. Thus, there would have been a total of 15 pairs of appendages: one pair of antennae, five pairs of biramous cephalic appendages, three pairs of thoracic appendages (one per segment) and 6 pairs of pygidial appendages (Fig. 5). Although the exact length of the antennae is unknown it does not seem very long, and

they are about 2 mm wide and not strongly tapered. There is no evidence of exopods, but endopods are consistently about 3–4 mm wide, and get thinner, down to 2 mm, in the last two pygidial endopods. The first cephalic exopod (Ce<sub>1</sub>) is the longest in the body, reaching 40 mm in length, with the rest basically getting shorter posteriorly from 30 mm to 19 mm in length (Table 1). Appendage tips reach half of the side in the thoracic-anterior pygidial area, increasing to two thirds towards the pygidial posterior-most pair. Fourteen pairs of circular to ovoid midgut glands, 2.5 to 4 mm across, can be recognised in the holotype (Fig. 3c), and six in the paratype, often 2 per body segment (Fig. 4c). They start at the level of Ce<sub>2</sub> and extend to Pe<sub>2</sub>–Pe<sub>3</sub> (Fig. 5).

**Remarks:** *Tafilocaris ordovicica* gen. et sp. nov. is placed in the Family Emucarididae Paterson, Edgecombe, García-Bellido, Jago & Gehling, 2010 due to presenting most of the diagnostic characters of the clade:



**Fig. 4.** Paratype of *Tafilocaris ordovicensis* gen. et sp. nov. (MGM-7755Xa + b), from the ‘Bou Nemrou’ site (top of the First Bani Group), early Sandbian, Tafilalt Biota. a. Concave counterpart MGM-7755Xb, low angle lighting from NW, reconstruction indicated in light grey. b. Latex of concave counterpart, MGM-7755Xb, whitened with magnesium oxide, low-angle lighting from NW. c. Composite interpretive drawing of part and counterpart. d. Convex part, MGM-7755Xb, low-angle lighting from NW. Abbreviations: ant: antenna; Ce<sub>n</sub>: Cephalic endopods; mgg: midgut glands; Ts<sub>n</sub>: Thoracic segments. Scale bars 20 mm.

tagmosis composed of cephalic shield with posterior margin nearly straight and transverse, short thorax of three or four segments, and elongate pygidium, longer than cephalic shield by 10–15 %, while the first thoracic segment is as wide as the cephalic shield, without constriction in width behind the cephalon. The cephalic shield across the three genera is very consistent in shape and proportions to the whole body. The thorax presents minor differences between the described taxa. Regarding the number of thoracic segments, there are three in *Kangacaris* and *Tafilocaris*, compared to four in *Emucaris*. In *Emucaris* the thoracic tergite boundaries are perpendicular to the longitudinal axis but are deflected posterolaterally in the pleural region of *Kangacaris zhangi*, a feature slightly more pronounced in *Kangacaris shui* (Zhang et al., 2012, fig. 1) and in *Tafilocaris*. The thorax and pygidium in *T. ordovicensis* lack the raised axial area, which is well defined in *Emucaris*

*fava* (Paterson et al., 2010, pl. 1, figs 1–2 and pl. 3, figs 1–4), but not so much in *Kangacaris zhangi* (Paterson et al., 2010, pl. 4, figs 1–2, text-fig. 7A–B; Paterson et al., 2016, fig. 3B). The pygidium of *T. ordovicensis* ends in an axial rounded tip, distinct from the other genera, with rounded to ogival posterior ends. The new Moroccan species lacks any evidence of hypostome, which is preserved in all other emucaridid species. *Tafilocaris* does not show evidence of the cephalic/pygidial border or doublure recognised in *Emucaris* and *Kangacaris zhangi*, but these are also absent in *Kangacaris shui*. Cephalic appendages seem quite similar in length and width among the three genera, with antennae relatively short across the family, but instead of the three pairs of postantennal cephalic limbs described for *Emucaris* and *Kangacaris*, *Tafilocaris* has five pairs of such limbs. The number of cephalic appendages varies considerably among arthropods but tend to be stable at lower taxonomic levels. However,

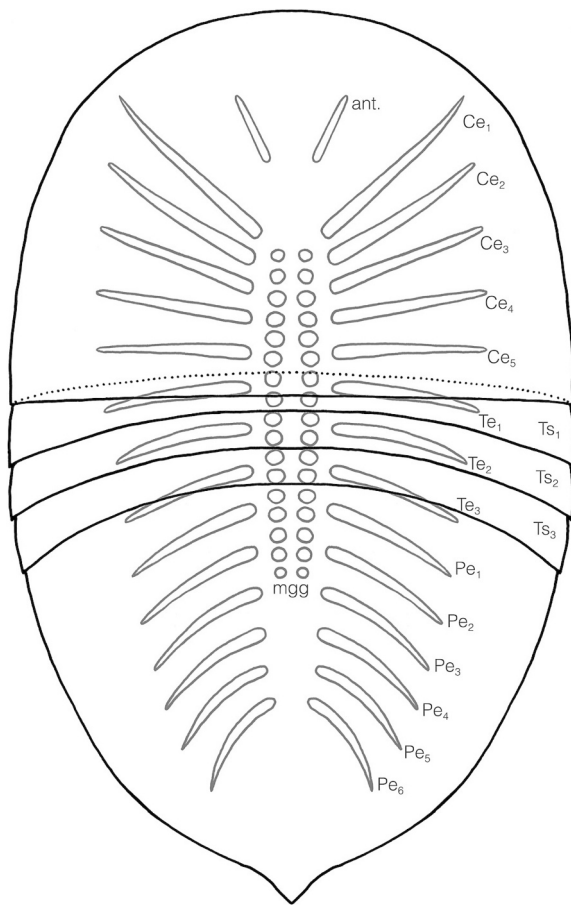


Fig. 5. *Tafilocaris ordovicica* gen. et sp. nov. from the ‘Bou Nemrou’ site (top of the First Bani Group), early Sandbian, Tafilalt Biota. Reconstruction in dorsal view, with internal and ventral structures (midgut glands, antennae and endopods, respectively) in light grey. Abbreviations: ant: antenna;  $Ce_n$ : Cephalic endopods; mgg: midgut glands;  $Pe_n$ : Pygidial endopods;  $Te_n$ : Thoracic endopods;  $Ts_n$ : Thoracic segments.

there are other exceptions to this when broad time ranges are concerned, such as the Family Leancoiliidae, where the Cambrian members like *Leancoilia* (Haug et al. 2012) and *Yawunik* (Aria et al. 2015) have 4 post-ocular appendages in the head: a pair of great appendage plus 3 biramous cephalic limbs, while the single Ordovician taxon, *Lomankus edgecombei*, has 5 post-ocular appendages: a pair of great appendage plus 4 biramous cephalic limbs (Parry et al., 2024). Besides three pairs of thoracic appendages, *Tafilocaris* also preserves six pairs of pygidial appendages, which are unknown for the Cambrian taxa, and these become shorter posteriorly. There is no indication of the total number of pygidial segments, but *Kangacaris* is estimated to have c. 12–13 segments, as defined by strong ring furrows (Paterson et al., 2010; Zhang et al., 2012). The only internal structure recognisable in the new taxon are the well-developed, paired midgut glands, which have not been identified in other members of the family. Although the cheloniellid genus *Duslia insignis* is quite common in these beds, *Tafilocaris ordovicica* gen. et sp. nov. is not only much larger (the former only reaches 110 mm in length, Chlupáč, 1988), but also lacks the fringe of close-spaced, flat spines sharply separated from the lateral and posterior margins of the cephalic shield and tergites by a continuous furrow, the procurved margin of the cephalic shield and the short pygidium (Fig. 2), as well as a pair of spiny furcal rami (Chlupáč, 1988).

## 5. Discussion

### 5.1. Phylogenetic affinities

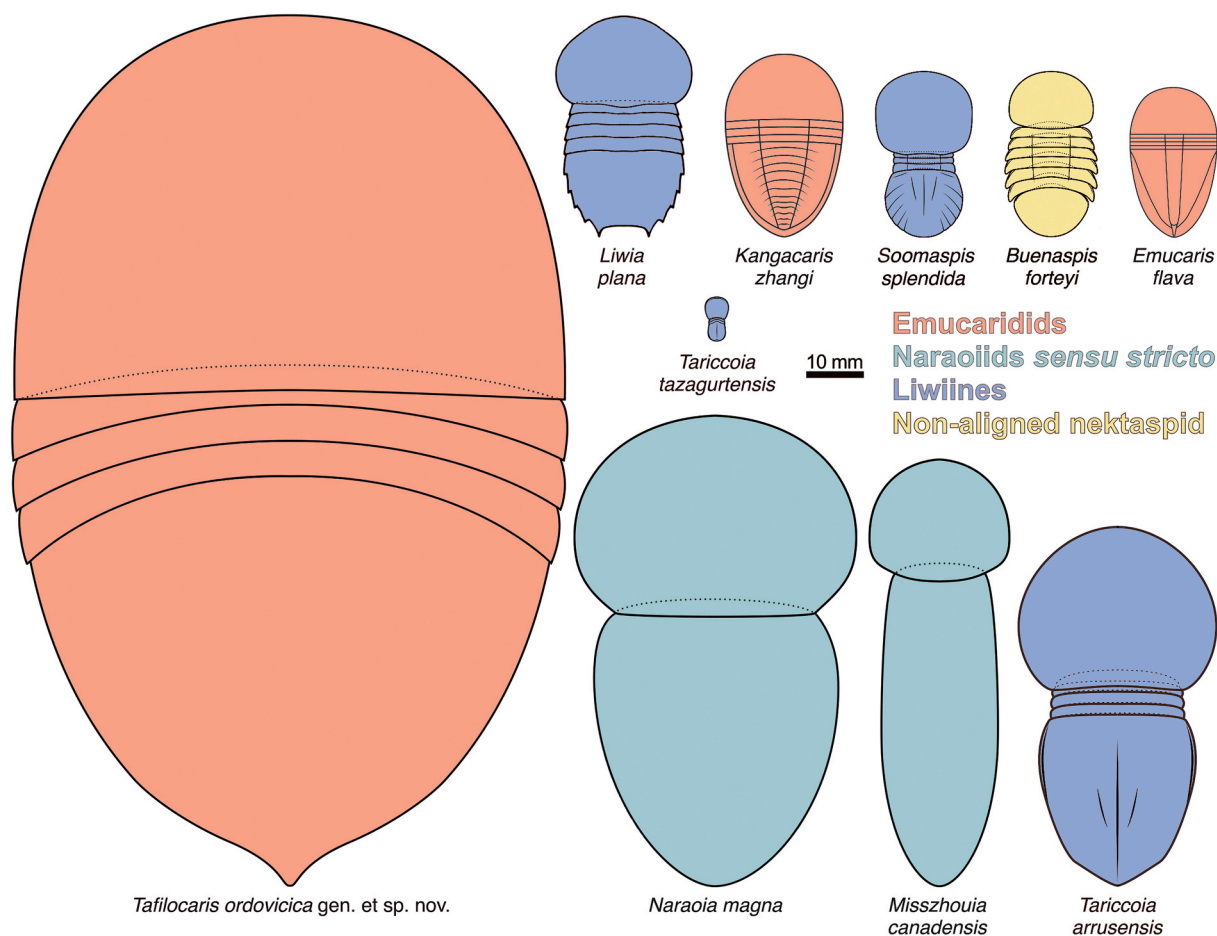
The new taxon does not fit into any of the other nektaspid groups. It cannot be assigned to the Family Naraoioidea Walcott, 1912, as that clade has a diagnostic two-part body, composed of a truncated ovoid cephalic shield, with convex posterior margin and a fused trunk shield, showing tapering of its anterior part relative to cephalic shield (Bond & Edgecombe, 2021). Despite previous literature discussing the relationships within the clade (Paterson et al., 2010, 2012; Mayers et al., 2019), Bond & Edgecombe (2021) indicate that their phylogenetic analyses return topologies for liwiine nektaspids (*Liwia*, *Tariccoia* and *Soomaspis*, but excluding *Buenaspis*) within the naraoioids, but argue that the monophyly of Liwiinae is sensitive to methods of character weighting, being contradicted in most of their analyses, so they treat it as an informal grouping. Notwithstanding, *Tafilocaris ordovicica* gen. et sp. nov. does not present the diagnostic characters indicated (Pérez-Peris et al., 2021) for the Family Liwiidae Dzik & Lenzion, 1988, namely a cephalic shield that is equal or longer than the pygidium, a constriction of the thoracic segments immediately behind the cephalon, and a cephalic shield which can overlap with up to two thoracic tergites. Additionally, liwiids predominantly have 4 thoracic tergites and the thoracic tergites and pygidium are considerably and consistently narrower than the cephalic shield (Fig. 6 and fig. 3 in Pérez-Peris et al., 2021). The ramifying gut diverticula –often with multiple levels of branching– typical of the cephalon and thorax of naraoioids, and purportedly present in *Tariccoia tazagurtensis* (Pérez-Peris et al., 2021, fig. 2), are absent in *Tafilocaris*, which has paired, subcircular midgut glands in the last few cephalic segments, all the thoracic segments and the first few pygidial segments. However, digestive glands have been recognized within gut diverticula of *Misszhouia longicaudata* (Zhang et al., 2007).

### 5.2. Size in Nektaspida

Emucaridids described to date are small (Fig. 6), with the Australian taxa reaching 27 mm in the case of *Emucaris fava* and 33 mm for *Kangacaris zhangi* (Paterson et al., 2010), while the Chinese *Kangacaris shui* is just 6.3 mm (Zhang et al., 2012). Most of the Nektaspida are around 30–60 mm long, with liwiids generally small: about 8 mm for *Tariccoia tazagurtensis* Pérez-Peris et al., 2021, 30 mm for *Soomaspis Fortey & Theron, 1994* and *Buenaspis Budd, 1999*, 40 mm for *Liwia Dzik & Lenzion, 1988*, and reaching 65 mm in *Tariccoia arrusensis* Hammann et al., 1990. The largest nektaspids described so far are the naraoioids, with *Misszhouia canadensis* up to 77 mm in length and *Naraoia magna* reaching 85 mm long (Mayers et al., 2019), both from the Cambrian Burgess Shale in British Columbia (Canada). This makes *Tafilocaris ordovicica* a true giant, since its 157 mm of maximum sagittal length make it from 5 to 25 times larger than its Cambrian emucaridid relatives and almost double the length of the largest nektaspids described so far (Fig. 6).

### 5.3. Distribution of Nektaspida

Although the Cambrian saw the heyday of nektaspids, with 6 genera (*Naraoia*, *Misszhouia*, *Liwia*, *Buenaspis*, *Emucaris* and *Kangacaris*) and at least 15 species, there are several post-Cambrian members in the clade. There are two species of *Tariccoia*: *T. arrusensis*, from the middle Berounian (lower Sandbian) Monte Argentu Fm., in Sardinia, Italy (Hammann et al., 1990), and *T. tazagurtensis* from the Upper Tremadocian levels of the Fezouata Shale, Morocco (Pérez-Peris et al., 2021). *Soomaspis splendida* has been described from the Hirnantian Cederberg Fm., in South Africa (Fortey & Theron, 1994). And there are two species of *Naraoia*: *N. hammanni* from the Oretanian (Darriwilian) of the lower part of the Šárka Fm. of the Czech Republic (Budil et al., 2003) and *N. bertiensis* from the Pridoli (Silurian) of the Bertie Fm., Ontario,



**Fig. 6. Nektaspid size comparison.** Size comparison of *Tafilocaris ordovicica* gen. et sp. nov. with the largest nektaspids known to date, plus the other emucaridid, liwiine and non-aligned Cambro-Ordovician genera (*K. z.* and *E. f.* modified from Paterson et al., 2010; *T. a.*, *T. t.*, *S. s.* and *B. f.* modified from Pérez-Peris et al., 2021 and *L. p.* modified from Dzik & Lenzion, 1988).

**Table 1**

**Body and appendage dimensions of *Tafilocaris ordovicica* gen. et sp. nov.** Appendage dimensions are based on holotype (ant–Ce<sub>4</sub>) and paratype (Te<sub>2</sub> to Pe<sub>6</sub>). Abbreviations: Ant: Anterior; ant: antenna; avg: average; c: cephalon; Ce<sub>n</sub>, Cephalic endopod; L: Length; l: left side; max: maximum; p: pygidium; Pe<sub>n</sub>: Pygidial endopod; Post: Posterior; r: right side; t: thorax; Te<sub>n</sub>: Thoracic endopod; Ts<sub>n</sub>: Thoracic segment; W: Width. \*: Estimated sector lengths based on gap between base of Ce<sub>4</sub> and Te<sub>1</sub>; \*\*: Preserved portion of appendage.

	Body dimensions (mm)			Body sector length (mm)		Appendage dimensions (mm)			
	Holotype	Paratype			Holotype		L**	W max	
L max	151.0	157.5			Ant. end–Ce <sub>1</sub>	30.0	ant.	12.5	2.5
W max	103.0	106.0			Ce <sub>1</sub> –Ce <sub>2</sub>	8.0	Ce <sub>1</sub>	40	3.5
Lc	–	68.0			Ce <sub>2</sub> –Ce <sub>3</sub>	6.5	Ce <sub>2</sub>	30.5	4.0
Lt	–	15.5			Ce <sub>3</sub> –Ce <sub>4</sub>	5.5	Ce <sub>3</sub>	16	3.5
Lp	–	74.0			Ce <sub>4</sub> –Ce <sub>5</sub> *	5.9	Ce <sub>4</sub>	26.5	3.5
Wc	–	103.0			Ce <sub>5</sub> –Te <sub>1</sub> *	5.9	Ce <sub>5</sub>	–	–
Wp	–	97.5			Te <sub>1</sub> –Te <sub>2</sub> *	5.9	Te <sub>1</sub>	–	–
					Te <sub>2</sub> –Te <sub>3</sub>	7.0	Te <sub>2</sub>	17.5	1.5
					Te <sub>3</sub> –Pe <sub>1</sub>	5.5	Te <sub>3</sub>	20.5	3.0
					Pe <sub>1</sub> –Pe <sub>2</sub>	6.5	Pe <sub>1</sub>	23.0	3.0
					Pe <sub>2</sub> –Pe <sub>3</sub>	7.5	Pe <sub>2</sub>	22.0	3.0
					Pe <sub>3</sub> –Pe <sub>4</sub>	8.5	Pe <sub>3</sub>	17.5	3.5
					Pe <sub>4</sub> –Pe <sub>5</sub>	5.8	Pe <sub>4</sub>	19.0	3.5
					Pe <sub>5</sub> –Pe <sub>6</sub>	5.0	Pe <sub>5</sub>	19.0	2.5
					Pe <sub>6</sub> –Post. end	37.5	Pe <sub>6</sub>	19.0	2.0
					Total	151.0			
<b>Thoracic segment max length</b>									
	l	r	avg						
Ts <sub>1</sub>	–	9	9						
Ts <sub>2</sub>	8.0	9.5	8.75						
Ts <sub>3</sub>	9.0	7.5	8.25						

Canada (Caron et al., 2004) and the Fiddlers Green Fm., Passage Gulf, New York State, USA (Bicknell et al., 2025), the youngest representative known for the group. *Tafilocaris ordovicica* joins these four genera, confirming the prediction (Bond & Edgecombe, 2021) that their phylogenetic analyses implied substantial ghost lineages within

nektaspids, and that those gaps in the fossil record of the clade would be filled with sampling suitable Ordovician facies, as has been demonstrated to be the case with the Tafilalt Lagerstätte.

When attending to the Emucarididae in particular, the new taxon extends their stratigraphic range by c. 57 Ma, from the Cambrian Series

2 Stage 4 Emu Bay Shale Lagerstätte, dated at 512 Ma (Betts et al., 2018), to the earliest Sandbian, Late Ordovician, ‘Bou Nemrou’ levels of the Tafilalt Biota (Kraft & Mergl, 1989; Gutiérrez-Marco et al., 2022b), estimated at ~455 Ma. It also expands the biogeographic distribution of the family from the original circum-tropical waters of Eastern Gondwana and South China to the high-latitude environments of Western Gondwana, making it a peri-Gondwanan clade.

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## Data accessibility

We confirm that all the data supporting the findings in this study are available within the article. 3D LiDAR of holotype and paratype parts of *Tafilocarid ordovicica* gen. et sp. nov. (MGM-7201a and MGM-7755a, respectively), from ‘Bou Nemrou’ site, top of the First Bani Group, early Sandbian, Tafilalt Biota of Morocco are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.29150873>.

## Declaration of AI use

We have not used AI-assisted technologies in producing this article.

## CRedit authorship contribution statement

**Diego C. García-Bellido:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Juan Carlos Gutiérrez-Marco:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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